ON THE RELATION OF ROOT GROWTH AND DEVELOPMENT TO THE TEMPERATURE AND AERATION OF THE SOIL

W. A. CANNON

There is great diversity in root development in desert plants. This is to be seen even in a single habitat where all of the species are apparently subject to similar environmental conditions. At the same time the same species, when growing in another habitat which differs as much as may be from the first one, may, however, still retain each its characteristic type of root-system. From these general facts it appears probable that there are environmental conditions, to a degree apart from the soil *per se*, which are held in common by otherwise unlike habitats, to which the developing roots react in characteristic manner and which thus may be of determinate importance in shaping the direction of root development. Among the most striking of such common factors, which fortunately lend themselves conveniently to experimentation, are soil aeration and soil temperature. Accordingly, in the preliminary experiments looking to a solution of the general problem relating to differences in root development, the reaction of roots to aeration and to temperature were taken up.

The reaction of roots to soil aeration was studied as an introduction to this work. It is apparent that such root-systems as lie close to the surface of the soil, as, for example, that of *Fouquieria splendens*, and especially *Opuntia versicolor* and other cacti, must hold a very different relation to the atmospheric air than such root-systems as are deeply placed. And, in fact, the cultures showed that the roots of *Opuntia* had a very definite reaction to an abundant supply of air. The possible bearing of these results on the placing of the roots in the soil, or on their typical development, will be treated in the concluding section of this paper. In the meantime, it will be sufficient to state that the results of the direct aeration experiments were not entirely consistent, for whatever reason, and they will be repeated at a future time. The attention, therefore, was turned, for the time, to a study of the reaction of roots to various soil temperatures and to a consider-

ation of the results as factors in the development of root types and in the distribution of the species.

Temperature of the Soil

The soil acts as a reservoir of heat due to the circumstance that there is usually less loss by radiation during the night than accumulates in the soil by day. It is, thus, a great temperature stabilizer. It is owing to these two facts that, to a large degree, soil temperatures are so important to the growth of the roots of plants, and, also, to plant growth in general.

As is well known the temperature of the soil varies considerably, especially with the depth beneath the surface. In the colder seasons, however, the superficial soil may register a lower temperature than the deeper soil. The amplitude of the daily and the seasonal variations in temperature, also, varies inversely as the depth. From the last condition it happens therefore that such root-systems as extend close to the surface are subject to maximum temperature changes, and, in this particular, their temperature relations form a marked contrast to the relations of the roots which lie deeply.

Among the factors which directly affect the soil temperature are its color, moisture content, and slant of the surface with respect to the position of the sun. Of these, the most important is the moisture content, for the reason that water has a specific heat about five times greater than the specific heat of the solid constituents of the soil.[1] In a later paragraph will be given a striking example of the lowering of soil temperature as a result of moistening by the summer rains. (See also, fig. 2.)

Although no extended studies have been made in the vicinity of the Desert Laboratory on exposure as a direct cause of temperature variation in soils it is clear that this factor is an important one and its importance is emphasized by the fact that the soil of the desert is poorly protected by vegetation. That the principle is of much significance can be easily shown. For example, having given a shaft of heat rays of a certain total energy E, and of a certain area A, the amount of energy impinging upon the surface of the soil will amount to E if the surface is of A extent, and this occurs when the surface lies at right angles to the incident rays. If the surface is at another angle than 90° the area is greater than A, and, for that reason, the amount

[1] Free, E. E., Studies in soil physics. Plant World **14**: 188. 1911.

of heat falling on a unit area would be less than E. Should, for instance, the surface lie at an angle of 45° to the incident rays, the area would be approximately 1.4 A, although there would be no increase in E, so that the amount of heat falling upon a unit area, in this instance, would be only about 70.7 per cent. of the maximum,

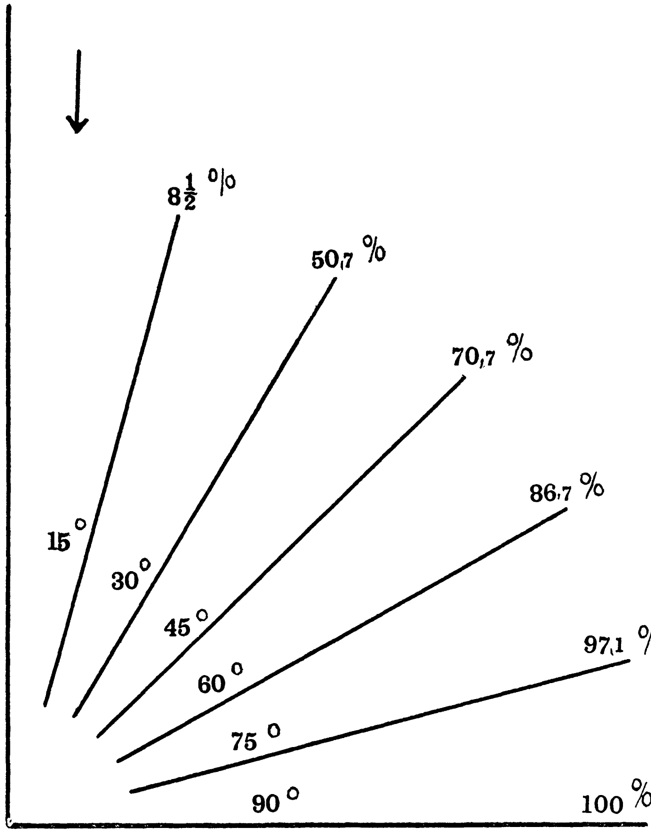

FIG. 1. Relative amount of heat per unit area falling upon the soil whose surface lies at the various angles given to the incident rays. The maximum amount received is that of a surface which is at right angles to the rays, as is indicated in the figure. The direction of the incident rays is that shown by the arrow.

that is, of the amount which would impinge on the surface were it at right angles to the source of heat. In short, it can be advanced that

the amount of heat falling upon the surface of the soil decreases with the decrease of its angle to the incident rays. The theoretical efficiency of different exposures, for several angles, is given in figure 1. It should be noted, however, as before suggested, that the amount of heat actually affecting the soil may hold different relations from that shown in the figure, for various reasons, some of which have been presented. In addition to these, it can be said, that the angle with the vertical is of itself important as a factor in that it directly affects convection currents.

[2] The general truth of the temperature-angle relation can be easily demonstrated, in a manner suggested by Prof. A. E. Douglas, University of Arizona, in the following experiment. Take a piece of heavy pine board, about 4 × 6 inches in size, and bore a shallow hole in the middle of one side. Connect this hole by a groove to one end. The groove is to carry the thermometer, whose bulb rests in the hole above mentioned. Fasten the board to uprights in such a manner as will permit it to swing on a horizontal axis, which, if continued, would reach the bulb of the thermometer. To the right hand upper corner attach a semicircular piece of white cardboard, ruled radially giving angles of 15°, 30°, and 45°. A nail is driven in the axis of the semicircle and allowed to project so that its shadow, falling on the cardboard, will give the angle of exposure desired. A thin sheet of copper is fastened over one side of the pine board, covering the thermometer. Finally, the wooden frame is enamelled white, and the copper sheet is painted black.

In order to check the observations made with the exposure pyrometer a black bulb thermometer, in vacuum, is used, and is read alternately with the other apparatus.

In practice, the test is made as follows. All instruments are allowed to come to shade temperature. Exposures to the sun of one minute each are made, and the instruments are allowed to return to the shade temperature, or close to it. The order of exposures, in the illustration given below, are as follows: 1, black bulb thermometer; 2, temperature at an angle of 90°; 3, black bulb; 4, temperature at angle of 60°; 5, black bulb; 6, temperature at angle of 30°; 7, black bulb; 8, temperature at angle of 90°; 9, black bulb.

The following data present results of a test on Feb. 6, 1915. The temperature rise in intervals of one minute and the time of each exposure are given.

Time	90°	60°	30°	90°	Black Bulb
10:44					5.1° C.
10:47	2.2° C.				
10:49		1.8° C.			
10:55					5.5° [1]
10:58			1.1° C.		
11:02					5.3°
11:06	2.3°				
11.08					5.3°

[1] The second reading of the black bulb thermometer was omitted.

At the Desert Laboratory there have been kept for several years three thermographic series giving the temperature of the soil. These series relate to three depths, namely, 15 cm., 30 cm., and 2.6 m.[3]

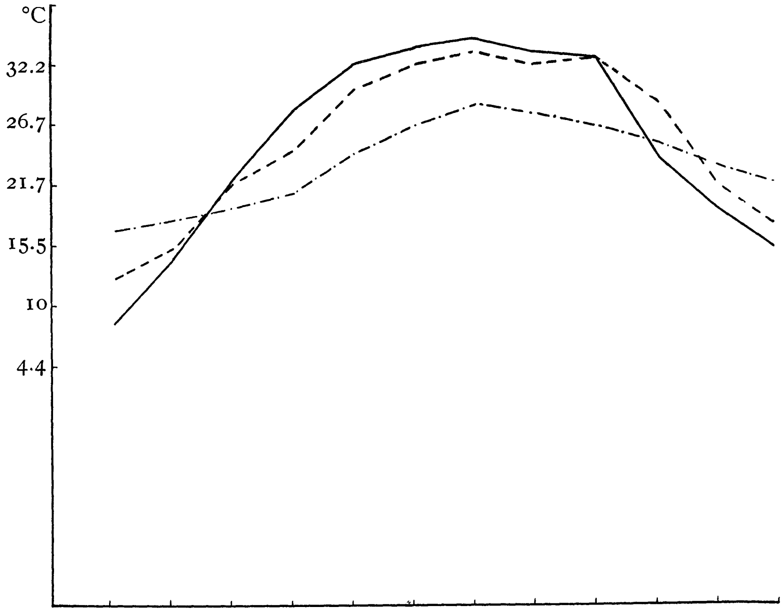

FIG. 2. Mean maxima soil temperatures, for different depths, at the Desert Laboratory, 1910. 15 cm. (———); 30 cm. (- - - - -); *ca.* 2.6 m. (—·—·—).

Since the soil temperatures obtained from the records have been discussed by several writers dealing with the botanical conditions of the region, only so much of them as will be necessary for illustrating the points brought out in this paper will be utilized. For this purpose the records covering a representative year, 1910, have been selected.

We will consider, in the first place, the temperature of the soil at a depth of 15 cm. In 1910 the mean maxima at this depth ran from

It will be seen that in the 24 minutes duration of the experiment the energy, as measured by the black bulb thermometer, changed little. By assuming the readings of the 90° angle as a basis, we see that the relative values are as follows: 90°, 100 per cent.; 60°, 81.3 per cent.; 30°, 50 per cent., which are close to the theoretical percentages as given in figure 1.

[3] The thermographic records for the depth of 2.6 m. are of the constant temperature chamber, but it is assumed that they represent, sufficiently well for the present needs, the temperature of the soil at the depth given.

8.1° C., in January, to 34.0° C., in July, and the mean minima temperatures for the same months were 3.9° C. and 30.8° C., respectively.

The mean maxima for 1910, at a depth of 30 cm., range between 12.2° C., in January, and 33.0° C., in July. During June, July, August and September, the mean maxima at this depth did not fall under 32.2° C. The mean minima temperatures, of midwinter and midsummer, were 10.0° C., and 32.2° C.

At a depth of 2.6 m. the mean maxima temperatures, in 1910, ranged between 16.6° C., in January, and 27.2° C., in July.

When we compare the mean maxima temperatures for the three depths we notice that, from April to August, inclusive, the shallowest soil is also the warmest. We see, also, that in September the 30 cm. horizon has the highest mean temperature, and, finally, that during the winter months the highest temperature occurred in the deepest soil. The relation of the mean maxima temperatures for the three depths is given, month by month, in figure 2.

In the preceding paragraphs the actual soil temperatures have been considered, but another viewpoint, also instructive, can be had by integrating the temperatures of the records used above.

The results of such temperature summation, of all soil temperatures above 10° C., are presented graphically in figure 3. It will appear at once that the amount of heat in the soil, at a depth of 30 cm. beginning with April, was greater than the amount at the 15 cm. horizon, although the latter provided the higher maxima. The maximum amount of heat, at the 15–30 cm. depths, was received in June, while the maximum amount at a depth of 2.6 m. was not received until August. The sudden drop in temperature at the shallower depths seen in July is associated with the occurrence of the summer rains which began at that time. However, the penetration of the moisture did not serve wholly to arrest the upward temperature movement at the depth of 2.6 m. until the following month.

In figure 3 is given, also, as horizontal lines, integrations of temperatures averaging 20.0° C. and 30.0° C. They show, among other things, what portion of the entire year has soil temperatures averaging more than 20.0° C. and 30.0° C., and at what depths. In a general way, also, the two lines delimit the seasons of root growth, and to a degree shoot growth, also, of the shallowly rooted and the deeply rooted plants. Thus, vegetative activity can be seen in *Prosopis velutina* Wooton in March–April, while shoot growth in *Fouquieria*

splendens Engelm. and in *Opuntia versicolor* Engelm, and active root growth also, as will appear below, does not occur until midsummer.

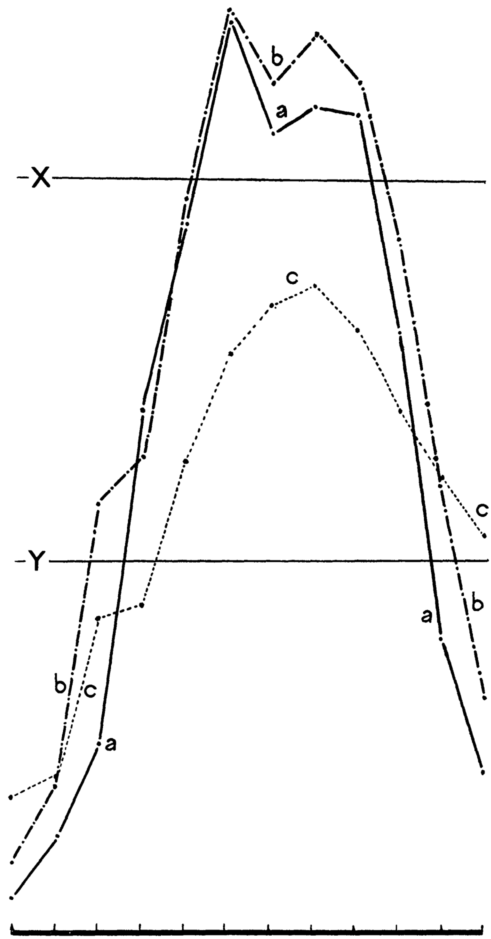

FIG. 3. Integration of monthly soil temperatures above 10° C., Desert Laboratory, 1910, at the following depths: 15 cm. (————); 30 cm. (—·—·—·); *ca.* 2.6 m. (- - - - -). The horizontal intersecting lines are integrations for an average temperature of 30° C. (*X*), and 20° C. (*Y*).

It should be interpolated here that root growth in the latter species, with shallowly placed roots, would take place in May–June were it

not for the circumstance that this is the arid foresummer when root growth, and, broadly speaking shoot growth, also, of shallowly rooted plants does not occur.

Enough has probably been given concerning soil temperatures to show that roots which occupy different soil horizons in the same habitat are exposed to widely different temperatures, not only in winter, when there is little, or no root growth, but also in summer when the growth of roots is most active. We will now consider how differences in soil temperatures influence the root growth rate of species having unlike root-systems, namely, *Prosopis velutina*, and *Fouquieria splendens* and *Opuntia versicolor*.

Relation of Growth Rate in Roots to the Temperature of the Soil.

In order to observe the response of roots of typical desert perennials to variations in soil temperature three species were selected for study. These, as before mentioned, were *Prosopis velutina*, representing the deeply penetrating root type, and *Fouquieria splendens* and *Opuntia versicolor*, representing the type of root-system that lies near the surface of the soil. The growth rate of the roots was observed in several forms of experiments, and in very many experiments, which were carried out at the Desert Laboratory and at the Coastal Laboratory at Carmel, and, it can be premised that, in spite of the widely different environmental conditions in the midst of which the two laboratories are situated, the general results of the cultures and experiments were in all instances consistent.

A brief sketch of the leading types of experiments and cultures will be sufficient for the present purpose. In one form of experiments seedlings and relatively small plants were grown in tubes of different diameters and different lengths. These were either exposed to the temperatures of the air, or were kept in thermostats of which the temperature was known. In another type of experiments the species were grown in a wooden or metal box with a sloping glass side, and which, again, was either permitted to follow the prevailing air temperatures, or was heated artificially. In addition to these methods of handling the plants, seedlings and young plants were grown in the garden both at Tucson and at Carmel. In the present paper only the leading results of these numerous as well as diverse experiments will be given.

As regards the general results of growing young plants, and seedlings of *Fouquieria splendens*, and of *Opuntia versicolor* in tubes exposed to air temperatures, it can be stated, in brief, that root penetration of 1 m., or over, was obtained in each species in a single season. The air temperatures to which the tubes were exposed, and to which they fairly closely conformed, ran as high as 35.0° C.

In the box culture the roots of the same species as above used attained, within a period of 10 weeks, a depth of 47 cm. The temperature of the vertical soil column was fairly uniform and varied from 10.0° C. to about 45.0° C. The long root growth was obtained where the temperature was 30.0°–35.0° C.

At the time the box culture, just referred to, was running, seedlings of Fouquieria and of Prosopis were grown in the garden (of the Coastal Laboratory) where the surface soil varied in temperature from 10.0° C., to 22.0° C. Ten weeks after the seeds germinated it was learned that the roots of Fouquieria had attained a depth of 15–20 cm., and that the roots of Prosopis, on the other hand, were 32 cm., or over, in length.

Thus the tube, the box, and the garden cultures, to give no more, indicated that relatively deep penetration of the soil might be expected in the cases of Fouquieria and Opuntia if the soil is of a suitable temperature, but if this is not the case, the roots of these plants remain near the surface. On the other hand, the roots of Prosopis, in a relatively short time and in relatively cold soil, attained to a considerable depth, which, in fact, was approximately twice that of the roots of *Fouquieria splendens* of the same age and growing under like conditions.

In the other tube cultures referred to, the rate of root growth was observed day by day, or hour by hour, as the case might be, and temperature readings, either of the soil of the tubes, or of the chamber where the tubes were placed, were made at the same time. In the first of the more exact tube cultures the period of observation extended over a period exceeding 10 weeks, during which time a thermographic record was kept of the culture chamber, and, also, the soil temperature of the tubes was taken. The leading results of this series is shown graphically in figure 4. It will be seen, in brief, that the growth rate of the roots varies directly with the variation of the air temperature to which the tubes were exposed. Beyond this, however, it appears that, at parallel temperatures, the roots of Prosopis grew more rapidly than did those of the two other species. It is to be seen especially that

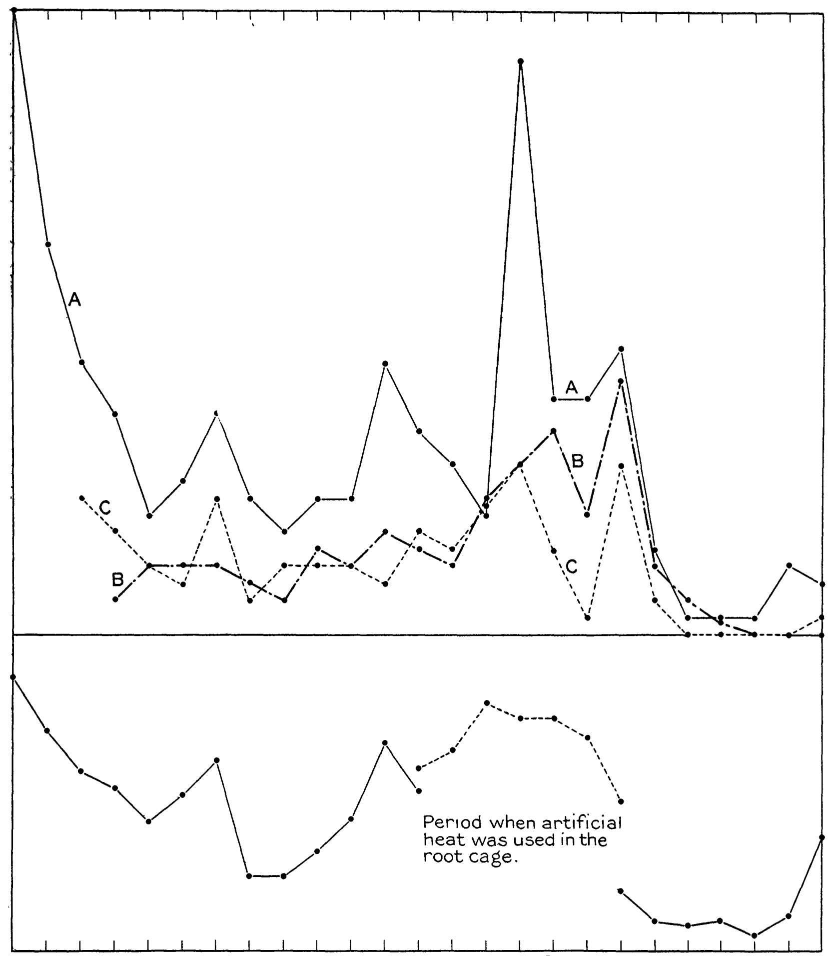

FIG. 4. Comparative daily growth rates of the roots of *Prosopis velutina* (*A*), *Opuntia versicolor* (*B*), and *Fouquieria splendens* (*C*), (much magnified), from November 12 to December 6, 1913. The lower curve gives the temperature summations above 10° C. in the root cage, and the detached curve is the summation when artificial heat was used in the cage. (From Year Book, Carnegie Institution, 1914.)

the growth rate of Prosopis roots at the lowest temperatures was relatively fast, and, also, that, at high temperatures, the roots of this

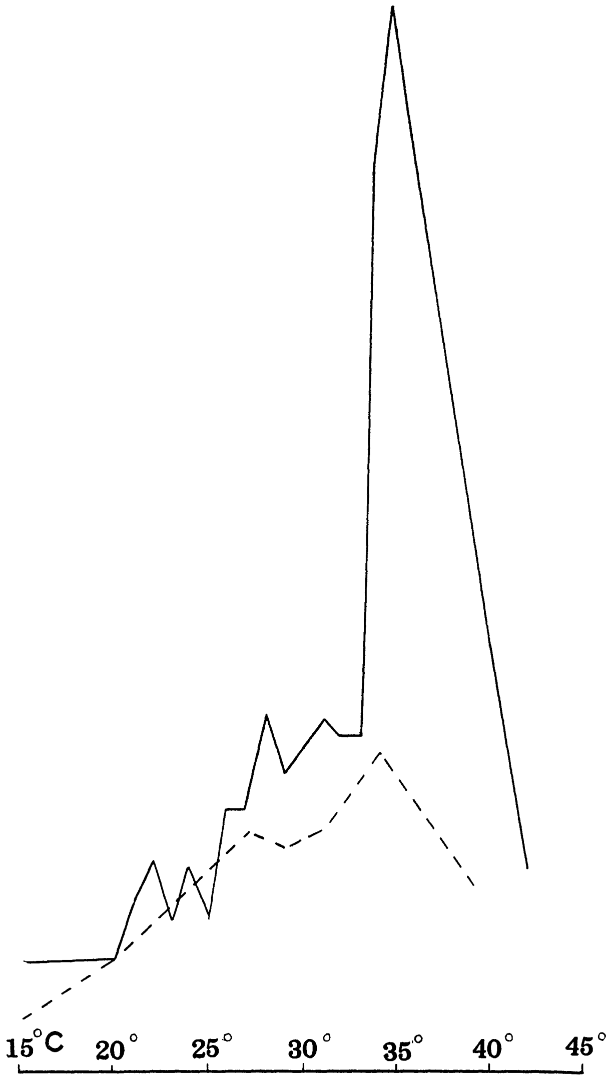

FIG. 5. Average hourly rate of growth of the roots of *Prosopis velutina* (———), and *Fouquieria splendens* (- - - - -) at the temperatures given (× *ca.* 100).

species grew at a more rapid rate than the roots of the other species. These points were subsequently verified in more precise cultures, as, also, they verify the previous observations already referred to.

The last series of experiments to be mentioned was that of tube cultures, also, in which special temperature control was used and in which thermostats of special design kept the tubes at temperatures between 20.0° C., or less, and 42.0° C., for as long periods as was desired. The readings of the root growth were usually made each hour at which time the temperature of the thermostat was also observed. In figure 5 appears the average rate of growth of the roots of *Fouquieria splendens* and *Opuntia versicolor*, taken from many readings, for the temperatures given. The growth rate is necessarily greatly magnified, but the comparative growth rates are consistent. To give an idea of the actual growth rates it can be said that the maximum average rate for Prosopis, reached at a temperature of 35.0° C. is 2.86 mm. per hour, and the maximum for Fouquieria was about 0.9 mm. per hour. The greatest growth rate observed in Prosopis roots was 3.0 mm. per hour. It will be seen that the rate of root growth falls away rapidly below 30.0° C. At 20.0° C. the rate for the roots of Fouquieria is very slow, practically ceasing at 15.0° C. In the case of Prosopis, on the other hand, a fairly active rate of root growth is maintained at 15.0° C., and, from other observations, it seems probable that growth continues at a temperature of 12.0° C. Thus the important fact is established that root growth occurs in Prosopis at a temperature so low as to be unfavorable for growth in Fouquieria, and *Opuntia versicolor*, also, although the root growth of the last species is not included in figure 5.

Root Development, Species Distribution, and the Reaction of Roots to the Soil Environment.

During the season of most active root growth, midsummer, there are three features in the root environment which are of especial importance, namely, the soil moisture, its temperature and aeration. It can be stated, in brief, that at this time, owing to the rains, the soil contains sufficient moisture for the developing plants, and, also, that the temperature of the soil, at the depths attained by roots, is suitable for their growth. Near the surface, in fact, as has already been shown, an optimum temperature for root growth obtains for a rather long period. Within limits, also, the moisture content of the soil increases, and the soil temperatures decrease with the depth beneath the surface. In addition to these features is the condition of the aeration of the soil. Air movements, of whatever kind, in adobe soil

are profoundly influenced by the addition of water. That there is active movement of air in air-dry soil, and that the movement is strikingly affected by moisture can be easily demonstrated. For example, a tube 30 cm. long, filled closely with air-dry adobe, requires, under the conditions of the test, only 0.5 cm. water pressure to cause an active air current to pass through. On the other hand, it is extremely difficult to add so little water that the air flow is not quite stopped. And, of course, if sufficient water is added to puddle the soil, it is impossible to force air through. It happens, therefore, with the rains of summer and the consequent thorough wetting of the soil, that the movements of the soil atmosphere are greatly modified, and the ingress and egress of air cut down to a marked degree, or entirely stopped.

It is apparent, from what has already been given, that roots which lie close to the surface of the soil are subject to the influence of an environment which is quite different from that affecting the deeply placed roots. From the standpoint of experimentation it is best to assume, also, that it is owing to unlike responses to environmental conditions, that the characteristic differences in the mature root-systems is largely, if not wholly, due. Thus, so far as the Fouquieria-Opuntia species treated in the present paper are concerned, it appears that low soil temperature is a factor which limits downward root growth, while, on the other hand, this factor affects the root growth of Prosopis very little. From observations on the behavior of the roots of *Opuntia versicolor*, growing in tubes, it appears, also that root branching in this species is very closely related to good soil aeration. Whatever may be the factors that control root branching in Prosopis, on the contrary, it is probable that abundant aeration is not an important one. Thus, root growth and root branching in Fouquieria-Opuntia take place mainly near the surface of the ground where the aeration-temperature conditions are favorable, and the root-systems of these forms are superficial. As the lower temperature of the deeper soil does not inhibit root growth in Prosopis, and as the roots are not so restricted in the aeration relation, deep penetration results. And, thus, through unlike physiological response there results strikingly dissimilar root growth and development.

As regards the relation of root reaction and root type to species distribution, however, it must be admitted that it is a subject upon which up to the present very little work has been done. Enough has

been accomplished on experimental and observational lines, however, to suggest the possible importance of the root relation in the distribution of species. The basis of the significance of the root factor in this connection lies in two general features, namely, in the root character itself and in the manner of response of roots to the soil environment. In the former case, especially in obligate deeply penetrating roots, the limiting factor appears to be only the depth of the soil. In such species, on the other hand, as have generalized roots and roots which are essentially shallowly placed, the condition is different. The limiting factors here relate to root response to such environmental soil factors as moisture, aeration and temperature.

From the position here taken, other distributional factors being equal, the species having the most plastic roots, and roots capable of the most catholic response to the soil environment, or both, should also be the most widely distributed, and conversely, species which are sharply limited in root growth by soil conditions, or whose roots are not plastic, should also have the most restricted distribution. So far as observations show the true condition, this conclusion is valid. From this it will appear at once that such factors as depth of soil, and soil moisture, aeration and temperature, are of the greatest importance. In addition there should be mentioned the exposure which, as already shown, greatly affects the temperature of the soil. It is of interest to note, also, that all of these, with the possible exception of the last named, are factors which are not commonly evaluated in a definition of a habitat and which do not immediately affect the shoots of plants.

Desert Laboratory, Tucson, Arizona.